

# White tail plumage and brood sex ratio in dark-eyed juncos (*Junco hyemalis thurberi*)

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**Abstract** Theory, empirical examples, and recently, proximate mechanisms point to the possibility of adaptive sex ratio adjustment in various organisms. General predictions state that a female should adjust her offspring sex ratio to maximize the benefits or minimize the costs of reproduction given her physical condition or current social and environmental conditions. I tested for an influence of male attractiveness on brood sex ratio in a population of dark-eyed juncos (*Junco hyemalis thurberi*) by manipulating a male's white outer tail feathers ("tail white"). Experimentally increasing male tail white did not significantly affect sex ratio, nor was premanipulated male tail white significantly related to brood sex ratio. However, the amount of white on the female's outer tail feathers, independently of female condition, was positively related to the number of sons in a brood. Determining how a female's potential genetic contribution to her sons' attractiveness influences offspring sex ratio should be a priority for future research.

**Keywords** Differential allocation · Sex ratio · Maternal effects · Dark-eyed junco

## Introduction

In most populations, parental investment is balanced between sons and daughters, a phenomenon explained by Fisher (1930) as the result of frequency-dependent selection. If investment is skewed toward sons, individuals will benefit from investing in daughters, and vice versa. This dynamic situation can both create and maintain an equal population sex ratio. Trivers and Willard (1973) recognized that daughters and sons generate different costs and benefits for their parents, and predicted that only females in good body condition could invest in the more costly sex. While Trivers and Willard (1973) focused on female body condition, other factors could influence the costs and benefits of sex allocation, including potential offspring attractiveness. The attractiveness (Cockburn et al. 2002) or differential allocation hypothesis (DAH; Burley 1986) proposes that the attractiveness of a female's mate will influence offspring attractiveness and therefore, optimal sex allocation. Specifically, the DAH predicts that females mated to attractive males should produce male-biased sex ratios. Differential sex allocation is expected when certain assumptions are met, namely, when attractiveness influences the future success of sons more than daughters, when attractiveness is heritable, and when variation in reproductive success is higher for males than for females (Burley 1986).

While adaptive sex ratio adjustment has been examined in many animal taxa (including both vertebrates and invertebrates), the potential for maternal control of sex allocation is particularly intriguing in birds; females are the heterogametic sex and could have fine control over sex allocation. Two recent reviews of the avian sex allocation literature concluded that birds may show facultative sex ratio adjustment, and specifically in relation to male quality or attractiveness (West and Sheldon 2002; Cassey et al. 2006). Most studies supporting the DAH in relation to sex ratio, however, are

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observational (e.g., Kölliker et al. 1999; Rathburn and Montgomerie 2004; Abroe et al. 2007). While correlations between male sexually selected traits and sex ratio suggest differential allocation, experimental manipulation of these traits is critical to assign causation and to control for confounding factors, such as assortative mating.

Only a few researchers have experimentally tested the effects of trait manipulation on offspring sex ratio. In blue tits (*Parus caeruleus*), females mated to males with naturally bright UV plumage had more sons, and when UV in these males (but not in less bright males) was experimentally masked the proportion of sons decreased (Sheldon et al. 1999; Korsten et al. 2006; see also Delhey et al. 2007). In zebra finches (*Taeniopygia guttata*, Rutstein et al. 2005, but see Burley 1986), barn swallows (*Hirundo rustica*, Saino et al. 1999), and dark-eyed juncos (*Junco hyemalis carolinensis*, Grindstaff et al. 2001) direct manipulation of male attractiveness did not affect sex ratio. Further experimental tests of the DAH in relation to sex allocation are needed.

I experimentally tested the DAH in dark-eyed juncos by measuring a female's primary sex ratio in relation to the number of white outer tail feathers (hereafter "tail white") on her mate. Juncos are an ideal system with which to test the DAH because tail white is easily manipulated and the assumptions of the DAH are met. First, males benefit more than females from the expression of tail white. In an aviary study, *J. hyemalis carolinensis* females preferred males with experimentally enhanced tail white (Hill et al. 1999), while males showed no preference for female tail white (Wolf et al. 2004). Natural tail white also relates positively to lifetime reproductive success in males, but does not affect female success (McGlothlin et al. 2005). Two additional patterns suggest tail white is a sexually selected trait: male juncos on average express more white than females, and in males, but not females, body size and tail white are positively related (Ferree, unpublished data; McGlothlin et al. 2005).

A second assumption of the DAH is that the focal trait is heritable; heritable variation in tail white has been detected in two junco subspecies, including the one studied here (*J. hyemalis carolinensis*, McGlothlin et al. 2005; *J. hyemalis thurberi*, Yeh 2004). Finally, the strength of selection for differential allocation depends on the strength of male competition (West and Sheldon 2002). While juncos are socially monogamous, male reproductive success varies to a greater degree than female reproductive success due to the presence of extra-pair fertilizations. Based on data from two junco populations roughly one-third of young are sired by an extra-pair male (*J. hyemalis carolinensis*, 28%, Ketterson et al. 1997; *J. hyemalis thurberi*, 29%, Ferree, unpublished data), confirming that males compete not only for a social mate but also for extra-pair opportunities.

While focusing on tail white's relationship with maternal investment, I also examined sex allocation in relation to body

size, as expressed by wing length. In many species, body size is a determinant of reproductive success (Yamaguchi et al. 2004; Karino et al. 2006), and also correlates with offspring sex ratio (Kölliker et al. 1999; Yamaguchi et al. 2004; Karino et al. 2006). In juncos, size predicts dominance; individuals with longer wings dominate smaller individuals in contests over food (Balph et al. 1979; Ketterson 1979; Holberton et al. 1989). Furthermore, the relationship between tail white and reproductive success is linked to body size. It appears that males with the longest wings dominate other males for access to females, and females choose among these males based on tail white (McGlothlin et al. 2005). I therefore considered wing length in this study because of its potential influence on sex allocation.

Finally, the DAH is traditionally applied to dimorphic species where sexually selected traits are inherited from the father (Sheldon et al. 1999; Saino et al. 1999; Korsten et al. 2006), yet in some species traits influencing male reproductive success are expressed in both sexes. For instance, both male and female juncos have white tail feathers even though current knowledge suggests that tail white only benefits males (Hill et al. 1999; Wolf et al. 2004; McGlothlin et al. 2005). In monomorphic or slightly dimorphic species, like juncos, heritable female traits that are advantageous to sons could also be significant predictors of sex ratio. Few studies, however, have examined sex ratio in relation to female traits other than body condition (see Ewen et al. 2004), and juncos are an ideal system with which to broaden this approach. I therefore considered the role of not only female condition (Trivers and Willard 1973), but also female tail white and wing length in predicting primary sex ratio.

In summary, I tested the DAH by: (1) enhancing tail white in a subset of males to determine if females increased their brood sex ratio with more attractive mates, and (2) determining if premanipulated male tail white correlated with brood sex ratio. I predicted that females mated to males with large amounts of white (experimentally enhanced or naturally) should produce a greater proportion of sons compared to females with less attractive mates. Male wing length and female tail white, wing length and condition could also positively relate to brood sex ratio because of their potential impact on the eventual reproductive success of sons.

## Materials and methods

### General methods

I studied the Oregon junco subspecies (*J. hyemalis thurberi*) at Sagehen Creek Field Station, University of California Natural Reserve (39°25' N 120°14' W, 1,944 m

elevation) in the 2003, 2004, and 2005 breeding seasons. Juncos began forming pairs and breeding at Sagehen in early to late May and began flocking again in mid to late July. Pairs renested after predation events that occurred early enough in the season, but were single-brooded. The study population averaged about 40 pairs.

Each year, I caught male and female adults using mist nets and baited traps. I gave each adult a USGS aluminum band and unique combination of plastic color bands and then measured flattened wing chord and tarsus. To assess female condition, I weighed females to 0.5 g and then calculated the residuals from a regression of female mass on body size (wing length). Residual mass should estimate the energetic reserves and hence condition of an individual (Brown 1996; Schulte-Hostedde et al. 2005). To assess the validity of using this approach, I confirmed that the relationship between wing length and mass was best described as linear (using curve estimation), and that there was no relationship between the resulting residuals and body size (Pearson's  $r=0.00$ ,  $p=1.0$ ,  $n=40$ ) (Green 2001; Schulte-Hostedde et al. 2005).

I scored tail white by visually estimating to the nearest 0.1 the proportion of white on each tail feather (Hill et al. 1999). Juncos usually have white on the three outer tail feathers and show the most variation on the third feather from the outside (rectrix 4). I estimated tail white on both right and left sides of the tail and summed these estimates for a measure of the total number of white feathers on the tail. For example, if an individual had two completely white feathers and one half-white feather on each side of the tail (2.5 tail white), it would have a total tail white score of 5.0. All references to tail white refer to this summed score. I verified the repeatability of visual estimation by making three independent estimates of tail white on 30 museum specimens (total tail white repeatability=95.8%,  $p<0.001$ ).

I located each pair's nest and any replacement nests after predation and monitored them every other day for hatching. For molecular sexing, I took 10–15  $\mu\text{l}$  of blood from the brachial wing vein of 5- to 6-day-old nestlings in 2003 and 2004. Because of high nest predation in all years, I bled nestlings from the jugular vein on day 1 or 2 in 2005. On the day after sampling, these young nestlings showed little to no signs of having been bled.

#### Tail white manipulation

Using a cut-and-paste technique (described below) junco males were given one of the following tail white treatments: increased tail white, control, or sham. I increased tail white in a subset of males in 2004 ( $n=15$ ) and 2005 ( $n=15$ ) to give them a total tail white score of 6.0 white feathers, 3.0 white feathers on each side of the tail. I chose this level of tail white to be within but at the maximum of the natural

range. Males in the study population averaged ( $\pm\text{SE}$ )  $4.75 \pm 0.06$  total white tail feathers ( $n=80$ ) with only two individuals having scores  $\geq 6.0$ . Sham males were treated in the same manner as increased-white males but had their own feathers cut and reattached (2004,  $n=17$ ; 2005,  $n=6$ ). Control males received no manipulation (2003,  $n=20$ ; 2004,  $n=9$ ; 2005,  $n=12$ ). Sham and control males were combined after I verified that sex ratios in these two groups did not differ (mean percent sons  $\pm$  SE, sham= $37.5 \pm 9\%$ , control= $37.5 \pm 15\%$ ;  $F_{1,15}=0.49$ ,  $p=0.50$ ), and will collectively be termed controls. Experimental and control males did not differ initially in tail white or wing length (Pillai's trace multivariate  $F_{2,57}=1.32$ ,  $p=0.28$ ). Females mated to experimental and control males also did not differ in tail white or wing length (Pillai's trace multivariate  $F_{2,51}=0.80$ ,  $p=0.92$ ), nor in subsequent clutch size ( $t_{78}=0.46$ ,  $p=0.65$ ).

The feather attachment process proceeded as follows and was similar to that used in previous junco studies (Holberton et al. 1989; Hill et al. 1999). I obtained white tail feathers from juncos in another population (Santa Cruz County, CA, USA), cut these feathers 1 cm from their base, and then hollowed out the feather shaft with a needle. On experimental males from the Sagehen population, I cut rectrix 4 at an angle 1.5–2 cm from the base. I applied a drop of superglue (Instant Crazy Glue) to the extra feather before pressing it over the feather stub and then spread a thin layer of glue around the attachment site. I trimmed newly attached white feathers to the length of original tail feathers, and the sham treatment did not noticeably shorten replaced feathers.

Trait manipulation was timed to not influence pairing (Burley 1988; Sheldon 2000), and therefore carried out after males had paired but before nest building. Breeding status was determined through daily observation and nest searching, as well as through a male's response to a recording of junco song. Males that had paired usually responded to a song tape readily and almost always in the presence of their mate.

#### Sex determination

To determine the sex of sampled chicks, I used the P2/P8 primer pair, which amplifies an intron of the *CHD1* gene on avian sex chromosomes (Griffiths et al. 1998). DNA was extracted using 24:1 chloroform-isoamyl and diluted as necessary to a concentration of approximately 50 ng/ $\mu\text{l}$ . I amplified the *CHD1* intron using polymerase chain reaction (PCR) ( $T_a=54^\circ\text{C}$ ) and ran the products along with a size marker on 3% Nusieve agarose gels. Bands were visualized with UV light after staining with ethidium bromide. Males had a single band from the Z chromosome and females had two bands, from both the Z and W chromosomes. I verified this method to be 100% accurate with 12 adults of known

sex (six males, six females). Finally, I repeated the above steps for individuals that I was initially unable to score.

### Statistical analyses

I used a goodness-of-fit test in Statistica 5.5 to first confirm that sex ratio data conformed to a binomial distribution. If the number of broods analyzed is small, this method can overestimate departures from a binomial distribution (Westerdahl et al. 1997), but if brood size itself is small (<4) randomization tests can also fail to detect a deviation (Ewen et al. 2003). I chose the goodness-of-fit test because my sample size was relatively large compared to junco brood sizes (mean of 3.6 offspring).

I examined the relationship between sex ratio and other variables using generalized linear models with binomial errors and a logit link in Genstat 9.0. In each model, the number of male offspring was entered as the response variable and the brood size as the denominator. The assumptions of linear regression, including homogeneity of variances (using Levene's test) and sufficient independence of predictor variables (all tolerance values >0.60) were confirmed.

The first model tested for an effect of tail white manipulation on sex ratio and included nest date, year, male tail white treatment, and their interactions. To evaluate the hypothesis that the treatment effect depended on characteristics of the parents, I added to the initial model premanipulated male tail white, to control for qualities that may be signaled by tail white, and wing length, as a measure of male body size. I also assessed the influence of female traits, specifically female tail white, wing length (body size) and condition, as well as all second-order interactions. I included both male and female traits in the same model to determine the independent influences of each variable. Finally, to further examine the influence of parental characteristics, I excluded broods of tail white enhanced males and analyzed control broods from all three study years.

I determined the significance of potential explanatory variables by calculating the change in deviance of the model with and without each term (Crawley 1993; Wilson and Hardy 2002). Deviance values are distributed approximately as a chi-square distribution (Crawley 1993) and only predictors creating a significant change in deviance were retained in the model. I then constructed a final model with the identified contributing factors (and tail white treatment if it was part of the full model) and similarly tested their contribution to this model. In all models, the dispersion parameter was approximately one (always < 1.25).

To focus on primary sex ratio, only completely sampled broods were included, and each adult was only represented once in analyses. For five returning females, I randomly

selected brood sex ratio from 1 year. None of these females remated with the same male in subsequent years. Although within-individual comparisons are powerful (Oddie and Reim 2002), samples sizes with complete brood sampling and morphological data were too small ( $n=3$ ) to permit such comparisons. I calculated power to detect a moderate effect of tail white treatment for nonsignificant results using G\*Power 3.0.3 (Faul et al. 2007).

## Results

### Population sex ratio

I sexed 234 nestlings from 70 broods in 2003–2005, and could not assign gender to 34 nestlings from 28 broods because they failed to hatch ( $n=15$  eggs), were predated before sampling ( $n=11$  nestlings), or because I was unable to obtain PCR products for those individuals ( $n=8$  nestlings).

Overall, 52% of offspring in the population were male, which did not differ from unity (binomial test,  $n=234$ ,  $p=0.59$ ); nor did the total percentage of sons differ from unity within any of the three study years (binomial test, 2003, 46%,  $n=58$ ,  $p=0.69$ ; 2004, 46%,  $n=74$ ,  $p=0.56$ ; 2005, 54%,  $n=102$ ,  $p=0.49$ ). Brood sex ratios are expressed as the percentage of sons, and the average brood sex ratio of 45% (95% CI, 37–53%) did not differ significantly from 50% (one sample  $t$  test,  $t_{42}=1.35$ ,  $p=0.18$ ).

### Main effect of tail white treatment

There was no difference in the percentage of male offspring between broods of enhanced tail white males and control males in either 2004 or 2005 [Table 1; mean percent sons (and 95% CI); tail white enhanced, 47.4% (35.4–59.4%,  $n=16$ ); control, 34.9% (20.1–49.7%,  $n=16$ )]. The power to detect a moderate treatment effect on sex ratio with this test was 67%. If I included all broods ( $n=43$ ), even those that were only partially sampled, power was increased to 71%. I still found no significant effect of tail white treatment (mean percentage of sons (95% CI); tail white enhanced, 51.9% (41.9–61.9%,  $n=22$ ); control, 39.3% (25.6–53.0%,  $n=21$ ), despite the apparent male bias in broods of tail white enhanced males.

### Effects of parental characteristics

To determine if the treatment effect was influenced by male and female characteristics, I added premanipulated male tail white and wing length, female tail white and wing length, and female condition to the initial model. For logistical reasons, female condition could only be calculated in one treatment year (2004), and all predictor variables could not

**Table 1** Results of generalized linear models testing the effects of tail white treatment and parental characteristics on primary sex ratio

Predictor variable	$\Delta D$	$p$
Tail white treatment		
Full model		
Year	0.12	0.73
Nest date	0.004	0.95
Tail white treatment	0.20	0.65
Tail white treatment $\times$ year	0.03	0.86
Tail white treatment and male and female characteristics		
Full model		
Year	0.26	0.61
Nest date	0.004	0.95
Male wing length	0.03	0.86
Female wing length	0.68	0.41
Female tail white	5.37	0.02
Premanipulated male tail white	1.63	0.20
Male tail white treatment	0.81	0.36
Final model		
Female tail white	6.79	0.009
Male tail white treatment	1.04	0.30
Control broods only: male and female characteristics		
Full model		
Year	0.92	0.34
Nest date	0.003	0.96
Male wing length	0.78	0.38
Female wing length	0.07	0.79
Female tail white	4.43	0.03
Premanipulated male tail white	1.78	0.18
Final model		
Female tail white	5.11	0.02

Removal of each predictor variable resulted in a change of one degree of freedom.  $\Delta D$  is the change in deviance when each predictor is excluded from the model. Tail white treatment, full model (residual deviance=46.30,  $df=3, 35$ ,  $p=0.96$ ). Parental characteristics, full model (residual deviance=26.81,  $df=6, 21$ ,  $p=0.09$ ), and final model (residual deviance=30.96,  $df=2, 29$ ,  $p=0.03$ ). Parental characteristics, control broods only, full model (residual deviance=32.68,  $df=5, 24$ ,  $p=0.08$ ) and final model (residual deviance=37.71,  $df=1, 31$ ,  $p=0.02$ ).

be fitted because of the small sample size. From a model including only male tail white treatment, year, and female traits (tail white, wing length, and condition), I found no evidence that female condition was related to sex ratio (change in deviance=0.66,  $p=0.42$ ,  $n=6$ ). I confirmed this result in a generalized linear model with female condition as the only predictor variable (change in deviance=2.41,  $p=0.13$ ,  $n=21$ ), and then excluded it from further analyses.

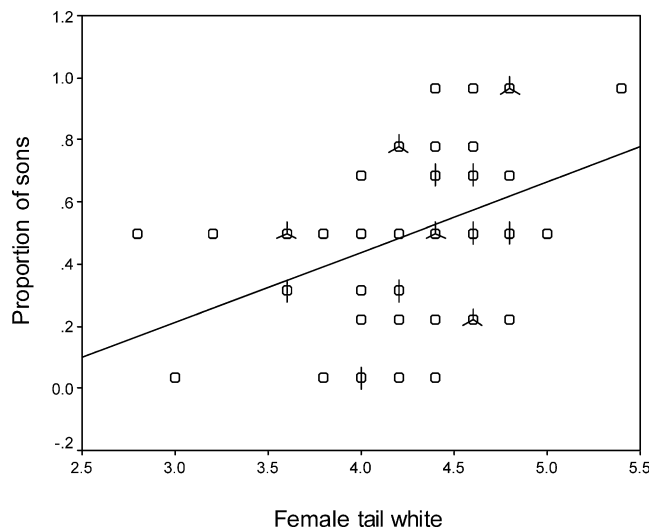
Controlling for parental characteristics did not change the effect of the tail white treatment. Furthermore, premanipulated male tail white was not significantly related to brood sex ratio, nor were male and female wing length (Table 1) or any interactions among the predictor variables (all  $p>0.15$ ). Female tail white, however, was significantly and positively correlated with sex ratio (Table 1).

To focus on the relationship between brood sex ratio and parental characteristics, I excluded experimental broods and included all control broods (2003–2005). Again, premanipulated male tail white was positively but not significantly related to sex ratio, and male and female wing length did not contribute significantly to the model (Table 1), nor was there an effect of year or any interactions (all  $p>0.14$ ). The tail white of the mother was significantly related to primary sex ratio (Table 1); as female tail white increased, the proportion of sons increased (Fig. 1).

## Discussion

### Male tail white

Females mated to males with experimentally enhanced tail white did not produce significantly more sons than females mated to control males, although the treatment effect and relationship with natural tail white were in the predicted direction. Statistical power to detect what appeared to be a difference between treatment groups was, however, relatively low ( $\leq 71\%$ ). An obvious criticism is that since many sexually selected traits are static, females may not respond to changes in their mate's quality after pairing (Mazuc et al. 2003). The lack of an experimental effect on sex ratio may reflect this constraint. In many studies, however, females do respond to changes in their mate's attractiveness within a breeding season (Sheldon 2000; Torres and Velando 2003; Korsten et al. 2006). Furthermore, experiments are necessary to randomize mating and gain the power to determine causation of female allocation.



**Fig. 1** Relationship between proportion of male offspring and female tail white (right plus left side of tail) for all broods in 2003–2005 ( $n=52$ ). Lines radiating from sample points represent sample sizes at particular sex ratio and tail white values

A female's sex allocation could be related to not only the attractiveness of her social mate, but also or instead to the attractiveness of any extra pair mates, and thus extra-pair paternity could affect my conclusions. Data on paternity collected in parallel with this study showed first, that rates of extra-pair paternity were almost identical between treatment groups (mean percent extra-pair young  $\pm$  SE; tail white enhanced,  $30.0 \pm 0.06\%$ ,  $n=23$ ; control,  $29.9 \pm 0.06\%$ ,  $n=23$ ). Furthermore, while premanipulated male tail white did not differ between treatment groups, the average manipulated tail white scores of the social male and extra-pair males (if any) of a given brood was greater at experimental broods than at control broods. This was true for all broods (mean average manipulated tail white  $\pm$  SE; tail white enhanced,  $5.86 \pm 0.06$ ,  $n=18$ ; control,  $4.73 \pm 0.11$ ,  $n=16$ ; Mann–Whitney  $U=8.5$ ,  $p<0.001$ ) and for only those broods with extra-pair paternity (mean average manipulated tail white  $\pm$  SE; tail white enhanced,  $5.76 \pm 0.11$ ,  $n=10$ ; control,  $4.81 \pm 0.19$ ,  $n=8$ ; Mann–Whitney  $U=7.0$ ,  $p=0.003$ ). These results confirm that the overall attractiveness of sires at broods of tail white enhanced males was greater than the attractiveness of sires at control broods, even when extra-pair paternity was considered.

In the junco population studied here, I predicted that females would bias offspring sex ratio based on their mate's tail white because tail white has a heritable component (McGlothlin et al. 2005) and because sons would benefit more than daughters from whiter tails (Hill et al. 1999; Wolf et al. 2004; McGlothlin et al. 2005). One potential reason females did not respond to tail white manipulation is that although tail white enhances male mating success in *J. hyemalis carolinensis*, its role may differ in *J. hyemalis thurberi*. Tail white expression varies among and within junco subspecies (Miller 1941; Yeh 2004; Ferree, personal observation), and tail white function may therefore also vary geographically. For example, song and tail white are both used by female juncos in mate choice (Hill et al. 1999), and perhaps the relative influence of these traits on male success, and hence, the strength of selection on tail white differs among junco subspecies. Such a scenario is being uncovered in blue tits (*Parus caeruleus*), where ultraviolet plumage is related to brood sex ratio in some populations (Sheldon et al. 1999; Korsten et al. 2006; Delhey et al. 2007), but at least in one population song characteristics are better predictors of sex ratio than plumage characteristics (Dreiss et al. 2006).

The fact that sex ratio is often correlated with male traits, yet less frequently affected by a single trait manipulation, suggests that correlations could result from selection on unmanipulated traits or perhaps a combination of traits. The use of multiple ornaments in female choice is common to many avian species (Møller and Pomiankowski 1993; Johnstone 1995; Abroe et al. 2007). If females assess male

attractiveness using multiple traits, such as body size, song, and tail white in juncos (Hill et al. 1999), manipulating a single trait might only weakly affect female investment. Assuming female juncos have the ability to adjust sex ratio, further work can clarify the relative influence, if any, of various male traits.

Selection for male-biased broods could be weak if trade-offs between male attractiveness and paternal care inhibit the ability of females to raise sons (Grindstaff et al. 2001). In another study, *J. hyemalis carolinensis* females did not bias sex ratio when mated to males with experimentally elevated testosterone (Grindstaff et al. 2001), even though testosterone appears to enhance male mating success (Enstrom et al. 1997; Raouf et al. 1997). Male junco fledglings are larger and heavier than females (Grindstaff et al. 2001; Nolan et al. 2002), making it likely that sons impose greater costs than daughters. Selection for females mated to testosterone-enhanced males to produce sons is probably weakened by the fact that testosterone negatively affects male care (Grindstaff et al. 2001; Stearns 1989). We do not understand the relationship between tail white and male care, and so the implications of such a trade-off are unknown for this study.

#### Female tail white

Female juncos did not produce male-biased broods when their mate expressed high tail white, even though sons should benefit from inheriting attractiveness (tail white). I found instead, that as their own tail white increased, females had increasingly male-biased broods.

One explanation for this result is that selection favors male-biased sex allocation when females themselves are "attractive". Tests of the DAH in relation to sex allocation have focused on the relationship between male attractiveness and brood sex ratio in sexually dimorphic species (Burley 1986; Sheldon 2000; Saino et al. 1999; Korsten et al. 2006), but maternal expression of sexually selected traits could also influence offspring attractiveness and therefore have predictive power. Specifically, I propose that when females, and not just their mates, express traits related to male attractiveness they should produce male-biased broods. In juncos, therefore, females with extensive tail white will be selected to produce sons, who will benefit more than daughters from the inheritance of this trait. This hypothesis could be tested in other monomorphic or slightly dimorphic species. Furthermore, in species where male deception is possible (if traits are not costly), adaptively allocating offspring sex based on maternal traits may prove to be more reliable than allocating based on male traits.

If the expression of sexually selected traits enhances female fitness because of the enhanced attractiveness of their sons, then selection could favor maternal "attractive-

ness”, perhaps through male mate choice. If attractiveness subsequently benefits both daughters and sons, a biased brood sex ratio may no longer be expected. This possibility can be evaluated in juncos. For example, if female tail white is passed from mother to son and enhances the mating success of sons, then directional selection should act on female tail white. In *J. hyemalis carolinensis*, male juncos do not select females based on tail white (Wolf et al. 2004), nor do individuals pair by tail white in this subspecies (McGlothlin et al. 2005) or in *J. hyemalis thurberi* (Pearson’s  $r=0.13$ ,  $n=65$ ,  $p=0.31$ ). In *J. hyemalis carolinensis*, tail white and wing lengths are positively genetically correlated and in males, correlational selection favors individuals with long wings and white tails. Because selection favors smaller females (McGlothlin et al. 2005), however, opposing selection on body size in males and females could constrain the evolution of tail white in females and subsequently explain the apparent lack of selection for female tail white. Similar trade-offs could exist in other systems and help maintain selection for females to bias sex allocation toward sons when they themselves have attractiveness traits.

The relationship between maternal condition and sex allocation is well-studied (Trivers and Willard 1973; Nager et al. 1999; Ewen et al. 2004), but the relationship between sexually selected traits expressed in females and offspring sex ratio has received very little attention. Several studies have included female size in explanatory models (Westerdahl et al. 1997; Saino et al. 1999; Leech et al. 2001; Westneat et al. 2002; Dowling and Mulder 2006), but size was not always related to male reproductive success. In an exception, a study of varied tits (*Parus varius*), which like juncos are only slightly sexually dimorphic, researchers investigated the relationship between sex ratio and male and female plumage traits and body size. Males express larger forehead and breast patches than females (Yamaguchi et al. 2004), but body size, as measured by tarsus length, best predicts male dominance and reproductive success (Yamaguchi and Kawano 2001). As expected, male tarsus length, and not plumage traits, related positively to brood sex ratio, but female tarsus length was not related to sex ratio (Yamaguchi et al. 2004). Further investigation will be required to test the role of female traits in the attractiveness hypothesis.

While my results showed that female tail white was the strongest predictor, it only explained a portion of the variation in brood sex ratio. Maternal condition and body size did not relate to sex ratio, but other factors such as female age and territory quality might influence sex allocation but could not be assessed (Cockburn et al. 2002). Furthermore, morphological traits like tail white could signal a female’s ability to raise sons, just as Trivers and Willard (1973) predicted body condition influences a female’s investment abilities. In this population, however,

female tail white did not relate to any measure of female care (incubation, brooding, and feeding) or female reproductive success (clutch size, hatching or fledging success) (Ferree, unpublished data), suggesting that tail white was not solely an indicator of female ability.

The relationship between female tail white and sex ratio in juncos was only correlative. Mechanistic studies will be essential for examining patterns between female traits and sex ratio, because female genotype, expressed by traits such as tail white, cannot be directly manipulated. In particular, hormonal variation may provide a proximate explanation for sex ratio patterns seen in field and laboratory studies (Love et al. 2005; Pike and Petrie 2006). For example, female Japanese quail (*Coturnix coturnix japonica*) implanted with corticosterone, a stress hormone, produced significantly female-biased sex ratios at laying (Pike and Petrie 2006). Corticosterone implantation yielded the same results in European starlings (*Sturnus vulgaris*) and females in poor condition had high corticosterone levels (Love et al. 2005). Along with maternal condition, corticosterone could covary with other female characteristics and traits. Research examining and manipulating corticosterone levels could elucidate the link between female tail white and the production of male offspring. Whether patterns between female traits and offspring sex ratio are adaptive also needs to be confirmed.

In conclusion, my results did not provide support for the differential allocation hypothesis with its traditional focus on male traits. Females mated to males with increased tail white did not produce significantly more sons than those mated to controls. More broadly, my findings indicate that female traits could influence sex ratio independently of male traits. Especially in monomorphic or slightly dimorphic species, like juncos, we might expect that the characteristics of both parents could influence the associated costs and benefits of investing in sons versus daughters. Detailed studies are needed to determine the relative role of female traits in explaining sex ratio patterns with particular emphasis on traits expressed by both sexes.

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